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THE DEGENERATE EYES IN THE CUBAN CAVE SHRIMP, PALÆMONETES EIGENMANI HAY.[1]

FRANK H. PIKE.

The blind shrimp whose eyes are considered in this paper is common in the pools of the sink holes and caves near Cañas on the Western Railway of Cuba. The material was collected by Professor C. H. Eigenmann, who described the localities in his account of "The Fresh-water Fishes of Western Cuba" ('03). The species was described by W. P. Hay, in his paper "On a Small Collection of Crustaceans from the Island of Cuba" ('03).

Material. — Four specimens were available for study. The general topographic relations were determined from a surface study of the different specimens. The histological detail was worked out mainly from one series of sections. The normal marine shrimp from Wareham, Mass., was used for comparison.

Methods. — The animals were killed in formalin and transferred to seventy per cent. alcohol. Preparatory to sectioning, the head was cut off and placed in Perenyi's fluid for about twenty-four hours, dehydrated, cleared in xylol, and imbedded in paraffin. Longitudinal horizontal sections were made. They were mounted on the slide by the water method, and stained with hæmalum and eosin. One specimen was killed in Vom Rath's fluid and stained with safranin. The eyes of the normal shrimp were depigmented by being placed in a ten per cent. solution of nitric acid for from twenty-four to seventy-two hours before being placed in Perenyi's fluid. The remainder of the technique was the same as for the degenerate eye.

[1] Contributions from the Zoölogical Laboratory of Indiana University, No. 58. This study was completed many months ago. Its publication has been delayed to secure good photographs of the critical sections. The material was collected with a grant from the Carnegie Institution.

The Gross Anatomy.

General External Appearance. — Like the cave crustaceans of southern Indiana and Kentucky, the Cuban shrimp is clear white or colorless. The antennæ are extremely long and the chelæ are relatively longer than in the out-door or normal species. The eye-stalks are plainly visible but not as prominent as in the normal species. In the cave-crayfish from southern Indiana and Kentucky the eye-stalks are almost hidden beneath the rostrum, when viewed from above. They are much more prominent in the present species.

Surface Views of the Eye-stalks. — I. Viewed from the side, with moderate magnification, the eye-stalks are seen projecting forward from the anterior lateral part of the head just below and to one side of the rostrum (Fig. 1). The eye-stalk is not termi-

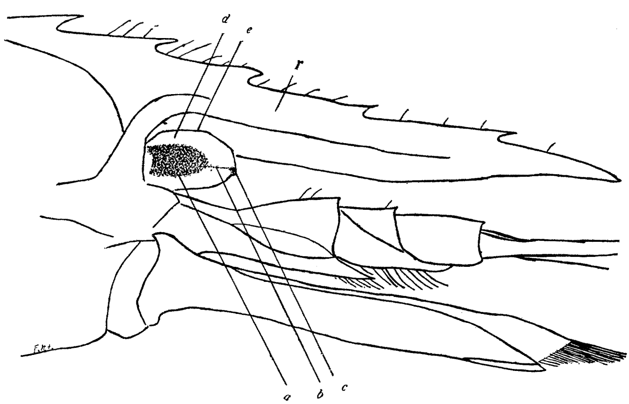

FIG. 1. Eye-stalk viewed from side. *r*, rostrum; *e*, eye-stalk; *a*, optic ganglion; *b*, optic nerve; *c*, retina; *d*, space filled with hæmolymph.

nated by a hemispherical cap as in the normal species, but by a peculiarly shaped, somewhat acute-tipped cone. The stalk is directed upward, forming a small angle with the horizontal. If the line drawn from the middle point of the base through the tip be taken as the long axis of the eye, the part of the stalk above this line will be at all points convex in outline. Beginning at

the tip, the part of the stalk below this line is slightly concave for about one-half the distance from the tip to the base of the cone. From this middle point of the base of the cone on to the base of the stalk, the outline is again convex.

The cuticula is clear white and partially transparent, with no trace of facets in the corneal region. There may be seen through it (*a*) a white mass, very nearly concentric in curvature with the outline of the eye-stalk, extending from the base forward a little more than two-thirds of the distance to the tip of the stalk, and terminating in a blunt cone; (*b*) a find strand running from a point a little below the end of this cone forward to (*c*) a small group of granules in the tip of the stalk. These granules appear to be spread over a small area on the proximal face of the cuticular tip, and taper to a narrower diameter where the thread joins them; (*d*) a space appears between the white mass (*a*) and the cuticula on the sides of the stalk. No trace of pigment is visible with any magnification. In sections these structures are seen to to be (1) the optic ganglion, (2) the optic nerve, (3) the remnants of the retina and dioptric apparatus, and (4) a space filled with hæmolymph, respectively.

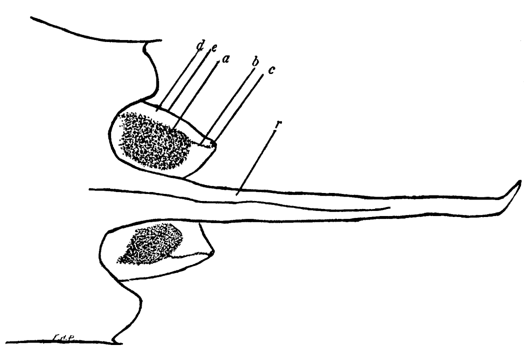

FIG. 2. Eye-stalk viewed from above. *r*, rostrum; *e*, eye-stalk; *a* optic ganglion; *b*, optic nerve; *c*, retina; *d*, space filled with hæmolymph.

Any great amount of shrinkage due to reagents would certainly break the fine strand of fibers running to the granules in the tip. I am inclined, therefore, to believe that the greater part of the space seen between the optic ganglion and the cuticula is normal in this eye.

II. Viewed from above, the outer side of the eye-stalk slopes inward toward the rostrum at an angle of 15 to 20 degrees to the longitudinal axis of the body. (Fig. 2.) The stalk terminates in a blunt, slightly rounded cone. The anterior mesial

edge of the stalk slopes inward and backward to the rostrum. The entire outline of the eye-stalk, when viewed from above, is singularly free from the graceful curvature of the normal eye-stalk. The same structures seen in the side view appear in this view. The tip of the eye-stalk is directed outwards away from the rostrum, and the optic nerve springs from the outer side of the anterior end of the optic ganglion. The granules are applied to the lateral surface of the stalk. The anterior end of the optic ganglion is more rounded than it is in the side view.

General Appearance in Sections. —The specimen on which the account of the minute anatomy here recorded is based, measured 17 mm. in length. The eye-stalk is 1,044 micra in its greatest length and 793 micra in its greatest width. The ratio of the length of the eye-stalk to its width is 1.3. The cuticula of the eye-stalk varies in thickness. It is 14.3 micra thick on the outer side of the stalk away from the rostrum, 10.9 micra in the region where the retinal elements are applied to it, and 7.2 micra on the inner side of the tip next the rostrum.

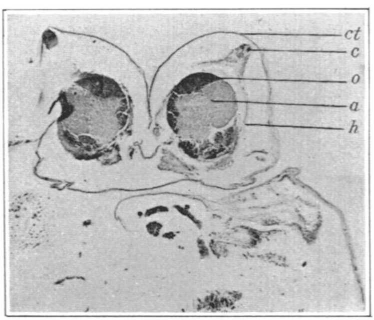

FIG. 3. Low power microphotograph of eyes of blind shrimp from above. *ct*, corneal cuticula; *c*, retina; *a*, fibrous portion of optic ganglion; *o*, cellular portion of optic ganglion; *h*, hypodermis.

In the left eye, the hypodermis and the retina have adhered to the tip of the stalk, but the optic nerve has broken so that the retina and the optic ganglion are separated. The retina is applied to the side of the eye-stalk. In the right eye, the hypodermis and the retina have pulled loose from the corneal cuticula, but the optic nerve is unbroken. (Fig. 3.)

The optic ganglion appears as a fibrous area surrounded by small cells with large, deeply-staining nuclei. The hypodermis has been torn loose from the sides of the eye-stalk and, in places, lies close to the optic ganglion. Transverse sections of the eyes of a specimen killed in Vom Rath's fluid show the hypodermis lying in contact with the cuticular wall.

In the right eye, a fibrous strand — the optic nerve — extends from the anterior outer part of the ganglion forward to the retinal elements. The optic nerve is bounded on each side by a layer of pavement cells with prominent nuclei. (Fig. 5.) In the right eye, the retinal elements are spread out rather loosely in the form of a fan, the apex of which is directed toward the optic nerve. Some spongy tissue, probably coagulated hæmolymph, appears on each side of the optic nerve between the bounding membrane and the hypodermis.

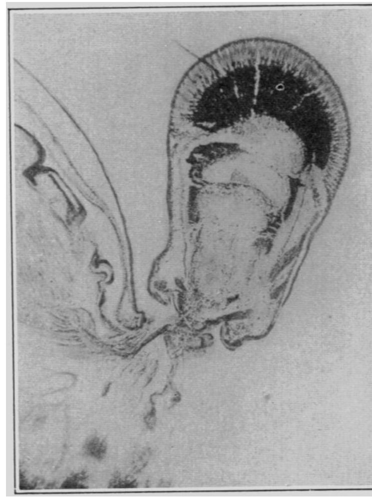

FIG. 4. Eye of normal shrimp; same magnification as Fig. 3.

Comparison of Normal and Degenerate Eyes. — Fig. 3 is from a photograph of the eyes of the blind shrimp. Fig. 4 is from a photograph of the author's preparation of a normal shrimp eye, made with the same magnification used in Fig. 3. It will be noticed (1) that the degenerate eye is much smaller than the normal eye, (2) that its optic ganglion is apparently a single mass of cells and fibers, and is not divided into parts as in the normal eye, and (3) that the retina and dioptric apparatus are represented by the merest vestiges of these structures as they exist in the normal eye.

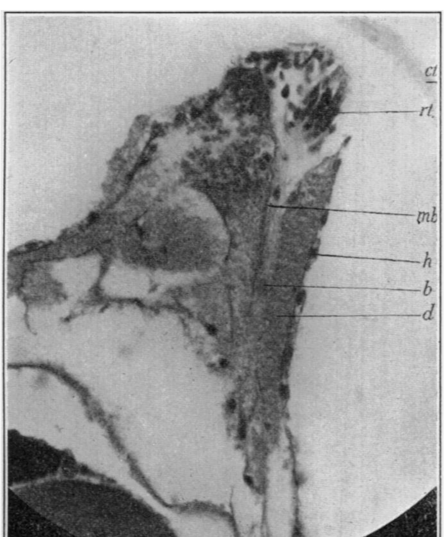

Fig. 5. Eye of blind shrimp. 4 mm. objective and 4 projection eye-piece. *rt*, retinula cells; *b*, optic nerve; *mb. l*, bounding membrane of optic nerve; *h*, hypodermis; *ct*; corneal cuticula; *d*, coagulated hæmolymph.

A few numerical results will make these contrasts more evident. There are present in each eye of a normal decapod about 2,500 ommatidia. (Parker, '95). Each ommatidium is composed of sixteen elements : two corneagen cells, four cone cells, two distal retinula cells, one rudimentary and seven functional proximal retinula cells, and one or more accessory pigment cells. In the retina of a normal eye there are, then, about 40,000 cells, about 22,000 of these being retinula cells. There are in the degenerate eye not more than 100 and not less than 50 retinula cells, and not more than ten or twelve cone cells. The cone cells in the normal eye outnumber those in the degenerate eye a thousand to one, and the retinula cells of the normal eye outnumber those of the degenerate eye by at least two hundred to one.

As stated above, the ratio of the length of the eye-stalk to its width in the degenerate eye is 1.3. In a normal crayfish eye I found this ratio to be 1.9. In the eye shown in Fig. 4, this ratio is 1.6. I do not know the range of variation in this ratio in the normal eye, but I feel safe in saying that the degenerate eye has decreased relatively more in length than in width.

The Minute Anatomy.

The Retina in the Left Eye. — The hypodermis consists of oblong cells closely applied to the cuticula and containing relatively large nuclei, Fig. 5. At the extreme tip, the cells become more spherical in shape and are slightly separated from the cuticula. The nuclei are less prominent than in the other hypodermis cells. Beneath these smaller cells is a layer of three somewhat larger spherical cells. Below these occurs a layer of two cells. All have small nuclei and clear cytoplasm. Two irregular masses, staining deeply with hæmalum but exhibiting no discoverable structure, lie, one on each side, immediately beneath the hypodermis and to one side of the clear cells above mentioned. Immediately beneath these dark masses are two other irregular, structureless patches staining diffusely with eosin and not at all with hæmalum.

Miss Seaton ('03) states that, in the compound eyes of Machilis, the cone cells do not stain readily with plasma stains. In some of my own preparations, the cone cells do not stain as readily

with a plasma stain as do some of the other tissues of the eye. Does this consideration, together with the position of these clear cells, afford us sufficient evidence to warrant us in regarding them as degenerate cone cells? I shall presently give a stronger argument in support of this conclusion. What the dark masses and the irregular patches of tissue represent I am not prepared to say. I am not certain that they posses any special morphological significance.

Beneath these structures is a group of larger cells with large, deeply staining nuclei. The nucleus occupies nearly all the space in the cell, there being only a narrow ring of cytoplasm within the cell wall. A plainly marked fibrous tract, the optic nerve, extends from these cells toward the optic ganglion. A fine membrane separates this fiber and cell tract from the hæmolymph or spongy tissue on either side. The large cells are, as I shall presently show, retinula cells.

The Retina in the Right Eye. — The tearing loose of the retina from the cuticula has destroyed the cone cells and the hypodermis at the tip so that no trace of either is visible. The looser arrangement of the large, deeply staining cells permits of a more accurate determination of their relation to the fibers of the optic nerve. With the oil immersion lens, the fibers can be traced up to these cells and can be seen ending in them. (Figs. 6, 7, *n* and *rt*.)

The objection may be urged that, since hæmalum is not a nerve stain, the fibers in question have not been shown to be nerve fibers. The reaction to iron hæmatoxylin is not as marked as in the fibers of the cephalic ganglion, but is still marked enough to indicate that they are nerve fibers. The strongest evidence that they are nerve fibers is their relation to the optic ganglion and their correspondence in position and relation to the nerve fibers in the normal eye. I believe that the simplest explanation open to us is that the fibrous strand represents the optic nerve.

Parker ('95) states that, in the normal decapod (*Astacus*) eye, the fibers of the optic nerve pass through the retinula cells and disappear in the region of the rhabdome. There is no instance known to me in which degeneration has caused a change in the

location of a nerve ending. I consider the deeply staining cells to be degenerate retinula cells. The cone cells have lost their distinctive characteristics much more than the retinula cells.

Summary. — The degenerate eye has a relatively shorter stalk than the normal eye. The corneal cuticula is thinner than that on the outer side of the eye-stalk. The optic ganglion appar-

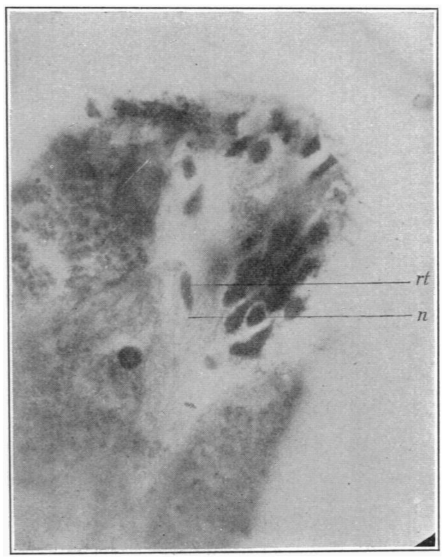

FIG. 6. Eye of blind shrimp. 2 mm. oil immersion objective, 4 projection eye-piece. x 1,000. *rt*, retinula cell in which a nerve fiber, *n*, may be seen to end.

ently consists of a single mass of fibers and cells. There is normally some space between the optic ganglion and the cuticula of the eye-stalk. The optic nerve, extending from the optic ganglion to the retina, is present. The retinula cells, in which the fibers of the optic nerve terminate, still persist. The vestiges of the cone cells may be, and probably are, present. The structures serving to distinguish light from darkness, probably being older phylogenetically than the structures concerned with the production of a definite image, are less degenerate than the latter. The active structures of the eye, represented by the retinula cells, have degenerated vastly more than the passive structures such as the cuticula.

Several questions arise to which no satisfactory answer can at present be given. (1) To what extent has the internal morphology of the neurones of the adult optic ganglion been modified by degeneration? (2) To what extent has the degeneration of the axones affected the cephalic ganglion of the animal? (3) What is the condition of the eyes in the embryo? The neurones of the

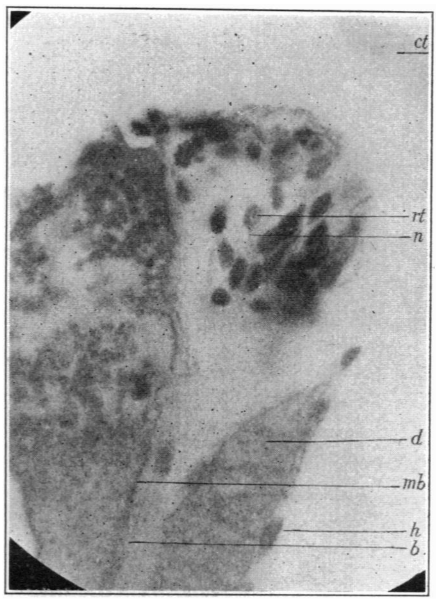

FIG. 7. Same eye as in Fig. 6, but different focus. x 1,000. *n*, a nerve fiber ending in *rt*, a retinula cell; *d*, coagulated hæmolymph; *mb*, bounding membrane of optic nerve; *b*, fiber of optic nerve; *h*, hypodermis; *ct*, corneal cuticula.

Microphotographs by Dr. D. W. Dennis, Earlham College, Richmond, Indiana.

optic ganglion seem to have degenerated so much that their internal morphology is enigmatical. No nuclear wall nor chromatin threads could be seen in any of them, even when stained with iron hæmatoxylin. It is an open question what the phylogeny of the decapod eye has been, and what bearing the present case of degeneration may have on the Law of Biogenesis. The embryological history might throw some light on this latter phase of the question, but it has been impossible so far to find embryos.

I wish to acknowledge the help received from the sources indicated in the bibliography. I am under obligations to Professor Eigenmann and to Dr. W. J. Moenkhaus for many suggestions and aid in completing the work. Professor Donaldson and Dr. Hatai of the University of Chicago have given valuable suggestions.

ZOÖLOGICAL LABORATORY,
INDIANA UNIVERSITY, August, 1904.

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